

# A Review of the Generic Divisions Within the Phyllidiidae with the Description of a New Species of *Phyllidiopsis* (Nudibranchia: Phyllidiidae) from the Pacific Coast of North America

by

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*Abstract.* The anatomy of *Ceratophyllidia africana* Eliot, 1903, and *Phyllidiopsis cardinalis* Bergh, 1875, the type species of their respective genera, is described. *Phyllidiopsis blanca* sp. nov. is described from the Pacific coast of southern California and Baja California. It differs from other species by its uniformly whitish coloration and low, poorly developed tubercles. Internally, it has a simple oral tube, without associated glands. The oral tube is elongate and convoluted. The buccal and gastro-esophageal ganglia are situated posteriorly from the circumesophageal nerve ring. The reproductive system is triaulic. The penis is lined with several rows of conical, chitinous spines.

The present species varies in its anal position. In one specimen the anus is located below the notum, while in the remaining five specimens it is located dorsally. Because the presence of a ventral anus is utilized to separate *Reyfriedia* Yonow, 1986, from *Phyllidia* Cuvier, 1797, the status of these genera is reviewed. The systematic position of *Phyllidiopsis* and *Ceratophyllidia* is discussed. Conflicting views of generic distinctions within the Phyllidiidae are also discussed.

## INTRODUCTION

The Phyllidiidae are a family of nudibranchs that are characteristic of tropical, Indo-Pacific shallow-water habitats. Seven species have been described from the Mediterranean Sea and Atlantic Ocean. These represent the only species known outside of the Indo-Pacific. No members of the family have been recorded from the Pacific Ocean east of the Hawaiian Islands. The first record of a phyllidiid from the Pacific coast of North America was that of *Phyllidia* sp. (as *Phellidia* sp., BEHRENS, 1980). This species is undescribed and its morphology and systematic placement are the subject of this paper.

The generic divisions of the Phyllidiidae have been the

subject of some disagreement. Part of the problem stems from the fact that the type species of two of the genera, *Phyllidiopsis* and *Ceratophyllidia*, have never been completely described. This study describes the anatomy of these species and discusses the relationships of the genera.

## DESCRIPTIONS

*Ceratophyllidia africana* Eliot, 1903

(Figures 1A, 2)

*Ceratophyllidia africana* ELIOT, 1903:250.

*Ceratophyllidia grisea* ELIOT, 1910:436, pl. 25, figs. 3-7, syn. nov.

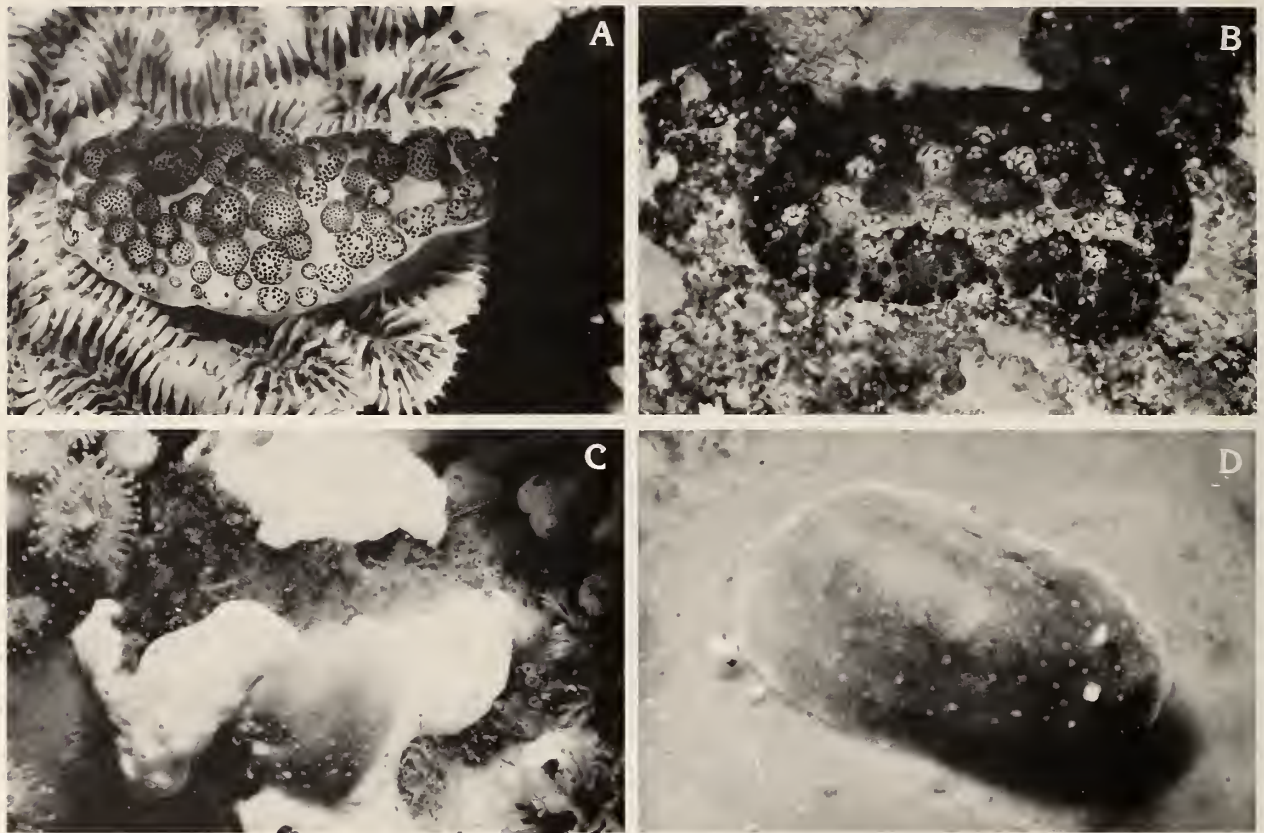


Figure 1

Living animals. A. *Ceratophyllidia africana* Eliot, 1903, Sodwana Bay National Park, South Africa, May 1981, photo by T. Gosliner. B. *Phyllidiopsis cardinalis* Bergh, 1875, Middle Camp, Aldabra Atoll, March 1986, photo by T. Gosliner. C, D. *Phyllidiopsis blanca* sp. nov., Islas San Benitos, August 1984, photos by Marc Chamberlin.

**Distribution:** This species is known only from the western Indian Ocean, where it has been recorded from Zanzibar (ELIOT, 1903), Coetivy Island in the Seychelles (ELIOT, 1910), South Africa (GOSLINER, 1987), and Aldabra Atoll, Seychelles (present study).

**Material:** South African Museum, Cape Town, SAM A 35625, one specimen, Nine Mile Reef, Sodwana Bay National Park, Natal, South Africa, 18-m depth, 20 May 1981, T. M. Gosliner. California Academy of Sciences, San Francisco, one specimen, CASIZ 063262, Passe du Bois, Aldabra Atoll, Seychelles, 10-m depth, 22 March 1986, T. M. Gosliner.

**External morphology:** The living animals (Figure 1A) were 20 and 30 mm in length. The general body color was yellowish white in the South African animal and grayish white in the Aldabran specimen. The densely perfoliate rhinophores were the same color as the body. The notum bears numerous soft, spherical papillae that are attached to the body by means of a short, slender stalk. The papillae

are readily autotomized when the animals are disturbed. The diameter of the papillae varies from 1 to 4 mm. In living material, the diameter of the papillae expanded and contracted. The papillae bear black pigment spots, which are restricted to their apical half. The anus is situated on the dorsal surface, near the posterior end of the animal. The lateral margins of the body, between the notum and foot, bear approximately 90 simple gill leaflets per side. The oral tentacles are largely separate to their bases and have a longitudinal groove along their outer margin.

**Digestive system (Figures 2A, B):** Immediately posterior to the mouth, the oral tube expands into a broad, thin-walled vestibule. The posterior end of the vestibule narrows into a thicker-walled, glandular oral tube. The oral tube is invaginable and, in its contracted state (Figure 2B), is contained entirely within the vestibule. The esophagus exits at the anterior end of the oral tube. The esophagus is elongate and highly convoluted. Also entering the oral tube are the ducts of a pair of large oral glands. The ducts

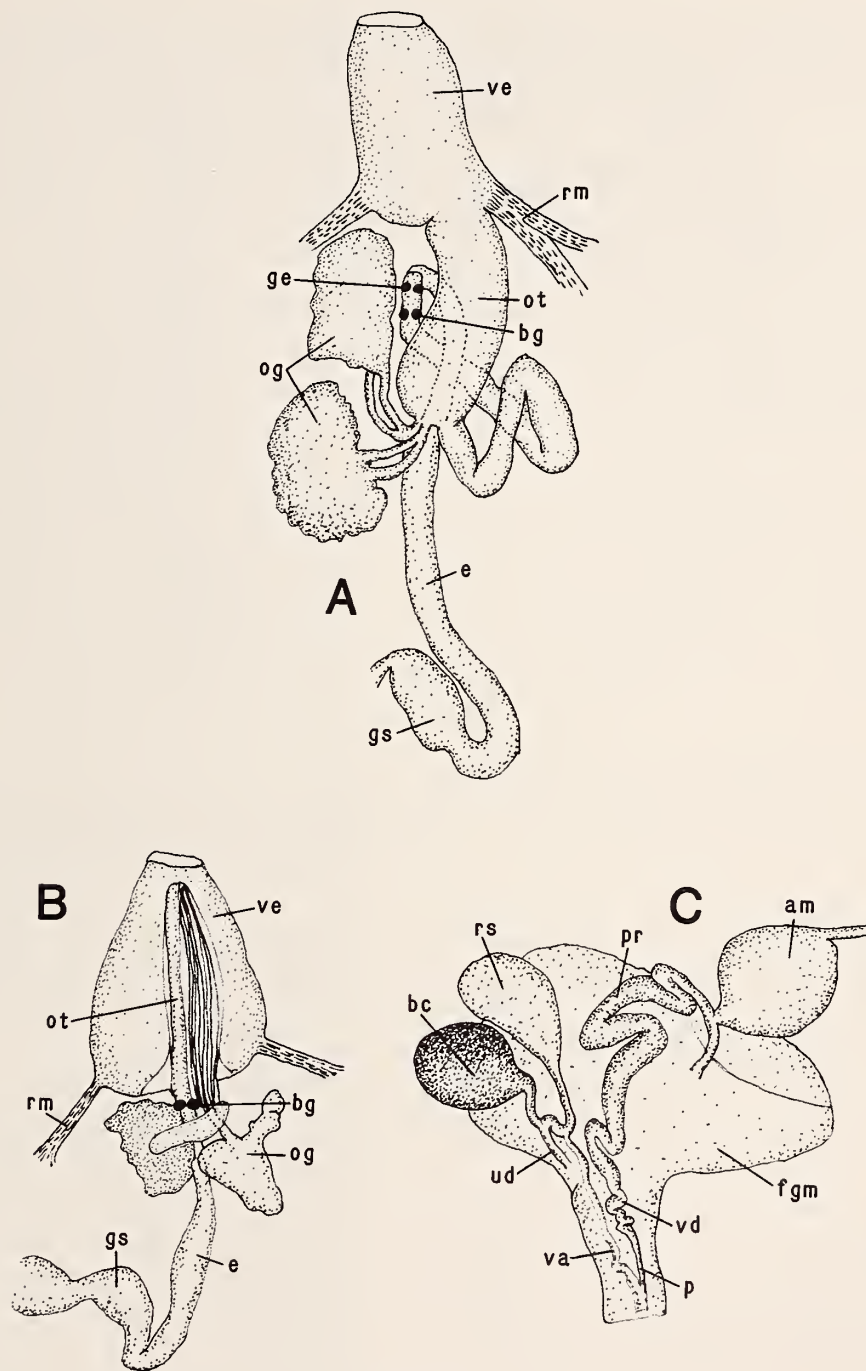


Figure 2

*Ceratophyllidia africana* Eliot, 1903. A. Digestive system retracted: bg, buccal ganglia; e, esophagus; ge, gastro-esophageal ganglia; gs, glandular segment of esophagus; og, oral glands; ot, oral tube; rm, retractor muscle; ve, vestibule. B. Digestive system everted, lettering same as A. C. Reproductive system: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; ud, uterine duct; va, vagina; vd, vas deferens.



of these glands terminate at the anterior end of the oral tube, adjacent to the esophagus. Posteriorly, the esophagus expands into a short glandular segment prior to its entrance into the thin-walled stomach within the digestive gland.

**Central nervous system:** The ganglia forming the circumesophageal nerve ring are highly cephalized, with complete fusion of the cerebral and pleural ganglia. The cerebropleural ganglia are appressed to each other, without a distinct commissure. The pedal ganglia are separated by a short commissure. The buccal and gastro-esophageal ganglia are attached to the circumesophageal nerve by long connectives. When the oral tube is completely invaginated within the vestibule these ganglia are situated immediately ventral to the circumesophageal nerve ring.

**Reproductive system (Figure 2C):** The arrangement of organs is triaulic. The ampulla is short and saccate, narrowing abruptly near its division into the oviduct and vas deferens. The oviduct is short and enters the female gland mass near the albumen gland. The uterine duct emerges from the female gland mass and joins the duct of the pear-shaped receptaculum seminis. The spherical bursa copulatrix is thin-walled and black in both specimens examined. It has an elongate duct and joins the duct of the receptaculum and continues proximally to the vaginal opening, adjacent to the penis. The vas deferens is prostatic distally and narrows into a muscular, ejaculatory segment. The proximal portion is devoid of any chitinous spines.

**Discussion:** *Ceratophyllidia africana* Eliot, 1903, was described from a single specimen collected from Zanzibar. ELIOT (1910) later described *C. grisea* from a single specimen collected in the Seychelles. He stated that *C. grisea* differed from *C. africana* in its gray rather than yellowish color and by having larger papillae that obscured most of the notum. No additional records of these species appeared until GOSLINER (1987) reported *C. africana* from Natal, South Africa. This specimen, examined in the present study, was yellowish in color, but had large, dense papillae as described for *C. grisea*. The specimen collected at Aldabra was grayish in color with sparser papillae. In both living specimens, it was noted that the diameter of the papillae could be altered by expansion or contraction. Dissection of these specimens demonstrated no internal differences between them, except in the state of contraction of the buccal apparatus. Therefore, *C. grisea* is here regarded as a junior subjective synonym of *C. africana*.

*Phyllidiopsis cardinalis* Bergh, 1875

(Figures 1B, 3)

*Phyllidiopsis cardinalis* BERGH, 1875:670, pl. 16, figs. 11–15.

**Distribution:** This species is known throughout the Indo-Pacific tropics, from Aldabra Atoll to the Hawaiian Islands (present study).

**Material:** California Academy of Sciences, San Francisco, CASIZ 063263, one specimen, Poipu Beach Park, Kauai, Hawaiian Islands, under rock, intertidal zone, 16 February 1986, Michael Gosliner. CASIZ 063264, one specimen, Poipu Beach Park, Kauai, Hawaiian Islands, under rocks, intertidal zone, 19 February 1986, Michael Gosliner. CASIZ 063265, one specimen, Passe Houreau, off Middle Camp, Aldabra Atoll, Seychelles, 2-m depth, 18 March 1986, T. M. Gosliner.

**External morphology:** The living animals (Figure 1B) were 12–24 mm long. The color is complex. The foot, anal papilla, rhinophores, and notum are yellowish. This pigment is overlain with papillae that are dark brown marginally, lighter brown to cream more medially. The spaces between papillae are off-white to mustard yellow. The raised central portion is finely papillate, off-white to cream. Three central raised portions on this ridge are dirty brown. The rhinophores are densely perfoliate. The lateral margins between the notum and foot bear numerous, simple, leaflike gill lamellae. The tubercles covering the dorsum are composed of several small rounded tubercles. The anus is situated medially on the dorsum near the posterior end of the body. There are approximately 110 leaflets per side. The oral tentacles are united for their entire length and possess a groove along both lateral margins.

**Digestive system (Figure 3A):** The most anterior portion of the oral tube is rugose and glandular. More posteriorly, it is smooth and curves anteriorly. Slightly more anteriorly to this point, the oral tube narrows into the esophagus. A retractor muscle inserts into either side of the oral tube at its junction with the esophagus. The esophagus is elongate and convoluted, passing through the circumesophageal nerve ring. Near its posterior limit the esophagus expands slightly to a segment that contains circular muscle fibers. Posterior to this it curves and enters the stomach within the digestive gland.

**Central nervous system:** The ganglia of the circumesophageal nerve ring are highly concentrated. The cerebral and pleural ganglia are almost entirely fused. The cerebropleural ganglia are appressed to each other, without a distinct, narrowed commissure. The pedal ganglia are separated by a short commissure. The paired buccal and gastro-intestinal ganglia are situated posteriorly, immediately anterior to the muscular portion of the esophagus (Figure 3A).

**Reproductive system (Figure 3B):** The saccate ampulla narrows abruptly into the postampullary duct, prior to its division into the oviduct and vas deferens. The oviduct is short and enters the distal portion of the female gland mass. The elongate uterine duct emerges from the female gland mass and joins the pyriform receptaculum seminis at the duct that joins the receptaculum with the spherical bursa copulatrix. From the bursa copulatrix the elongate vaginal duct runs proximally to a joint gonopore with the

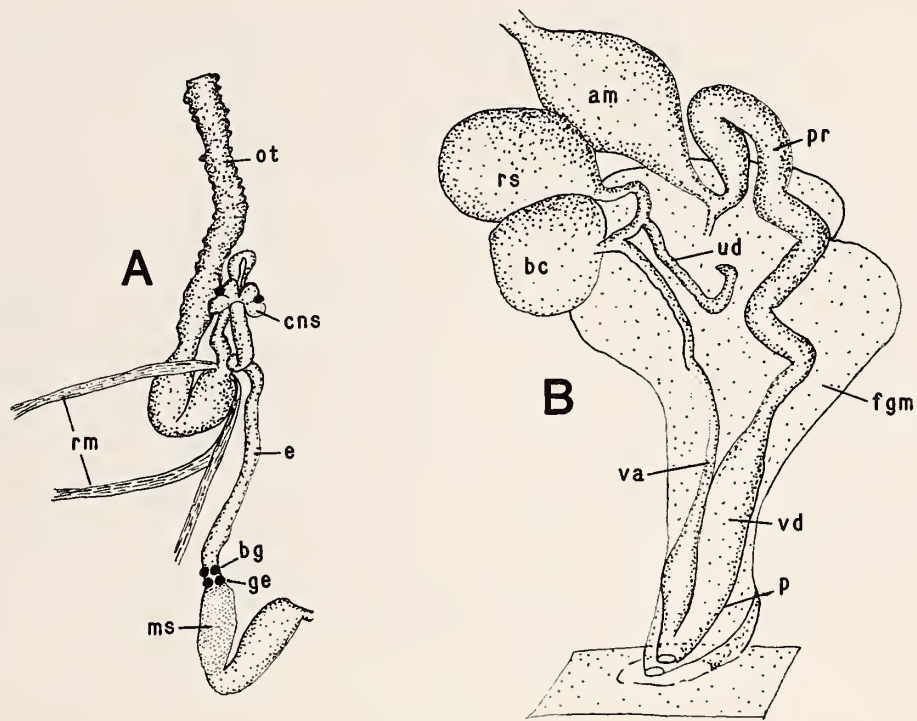


Figure 3

*Phyllidiopsis cardinalis* Bergh, 1875. A. Digestive system: bg, buccal ganglia; cns, central nervous system; e, esophagus; ge, gastro-esophageal ganglia; ms, muscular segment of esophagus; ot, oral tube; rm, retractor muscles. B. Reproductive system: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; ud, uterine duct; va, vagina; vd, vas deferens.

penis. The vas deferens is prostatic distally and widens into a muscular portion. There are no cuticular spines associated with the penis.

**Discussion:** *Phyllidiopsis cardinalis* Bergh, 1875, is the type species of the genus. Some aspects of its morphology were described in the original description, but details of the reproductive anatomy were not examined. The digestive system is characterized by a short muscular segment at the posterior end of the esophagus. As far as is known, this is the only member of the genus to have this structure. Another species, *P. tuberculata* Risbec, 1928, is similar to the present species in that it also has compound tubercles and has similar coloration. As suggested by PRUVOT-FOL (1957), this species is probably synonymous with *P. cardinalis*. In RISBEC's (1928) description of this species, he indicates that a large salivary gland is present. This is likely the blood gland rather than a salivary gland.

*Phyllidiopsis blanca* Gosliner & Behrens, sp. nov.

(Figures 1C, D, 4, 5)

*Phellidia* (sic) sp.: BEHRENS, 1980:100, fig. 144.

*Phyllidia* sp.: BEHRENS & GATEWOOD, 1986:139.

**Type material:** Holotype, California Academy of Sciences, San Francisco, CASIZ 063266, San Nicolas Island, ¾ mi (1.2 km) S of Sand Spit Light, 33°12'N, 120°25'W, CIRP Station SNI-2, 40 ft (13 m) deep, 22 October 1982, Jack Engle, 25 mm preserved. Paratypes, CASIZ 063267, 5 specimens, Isla San Benitos, 28°20'N, 115°40'W, 11 m deep, 6 August 1984, Jim Gatewood and Marc Chamberlin.

**Distribution:** Pacific coast of California and Baja California, Mexico, from Santa Barbara Island to Isla San Benitos. Specimens examined in this study were collected from San Nicolas Island and Isla San Benitos. Photographs of specimens made available to us indicate that this species occurs at least as far north as Santa Barbara Island and from several localities within this range.

**External morphology:** The living animals (Figures 1C, D, 4A) are 10–25 mm long. The general body color is white to grayish white. The sparsely perfoliate rhinophores are the same color as the body. The notum bears numerous soft, low tubercles. Although varying in diameter, these tubercles are more or less evenly dispersed over the notal surface. No gradation in size occurs as the tubercles near the notal margin. In five of the six specimens



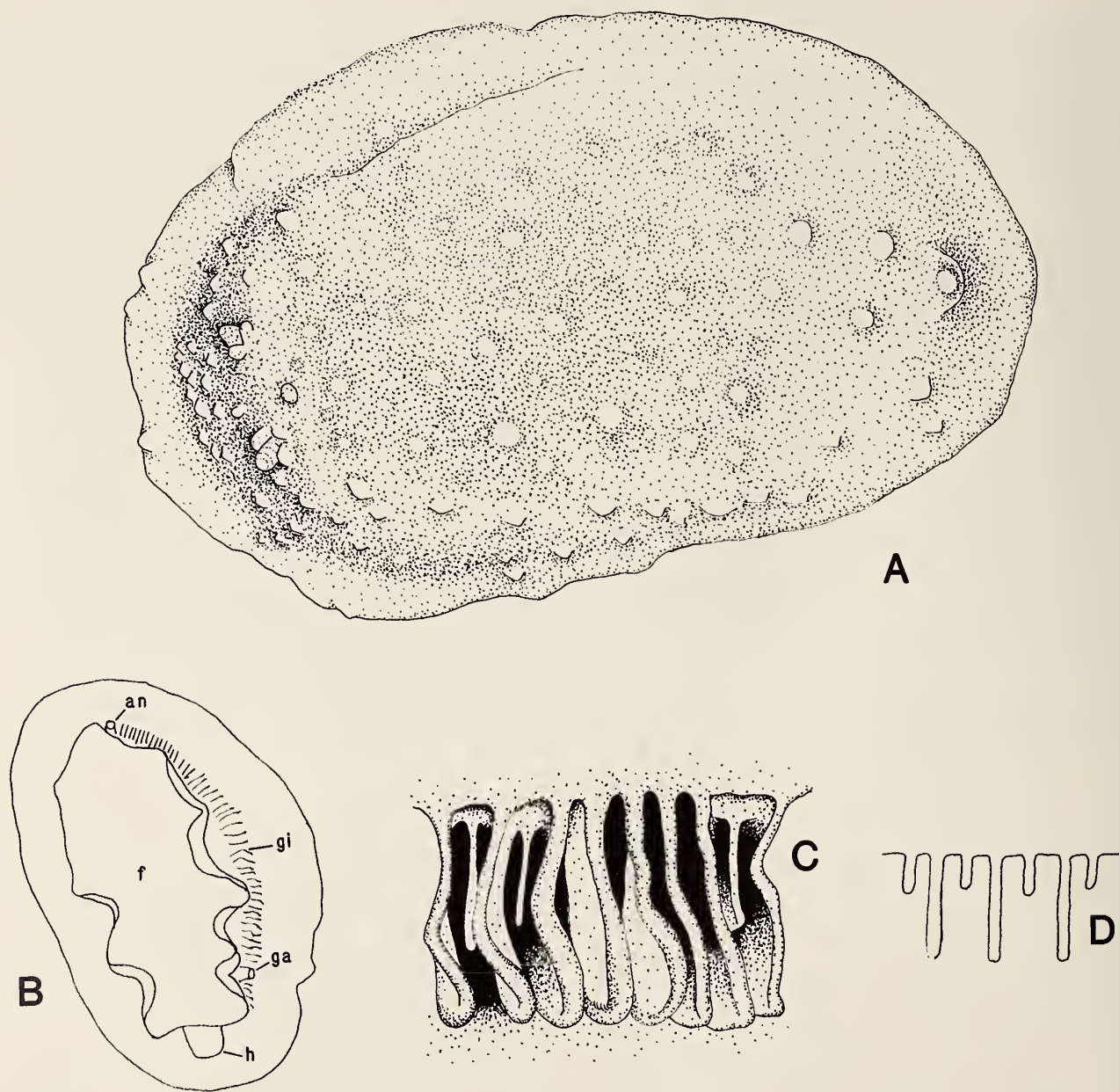


Figure 4

*Phyllidiopsis blanca* sp. nov. A. Dorsal view of living animal. B. Ventral view of preserved specimen with ventral anus: an, anus; f, foot; ga, genital apertures; gi, gills; h, head. C. Section of gills. D. Schematic view of gills, showing alternation of large and small gill filaments.

examined, the anus was located dorsally, near the posterior end of the animal. In the sixth specimen (Figure 4B) from Islas San Benitos, the anus is located posteroventrally on the hyponotum. The gills are arranged laterally, between the notum and foot. It is difficult to establish the exact number of gill leaflets, as the gill is a series of large lamellae irregularly interdigitated by smaller gill leaflets (Figures

4C, D). A count of the major gill elements in the holotype indicates that they may not be bilaterally equal, with the left side bearing about 70 leaflets and the right side approximately 60. This is due to the interruption of the leaflets on the right side, in the vicinity of the gonopores. Remnants of oral tentacles are present as grooves along either side of the flattened, quadrangular head.

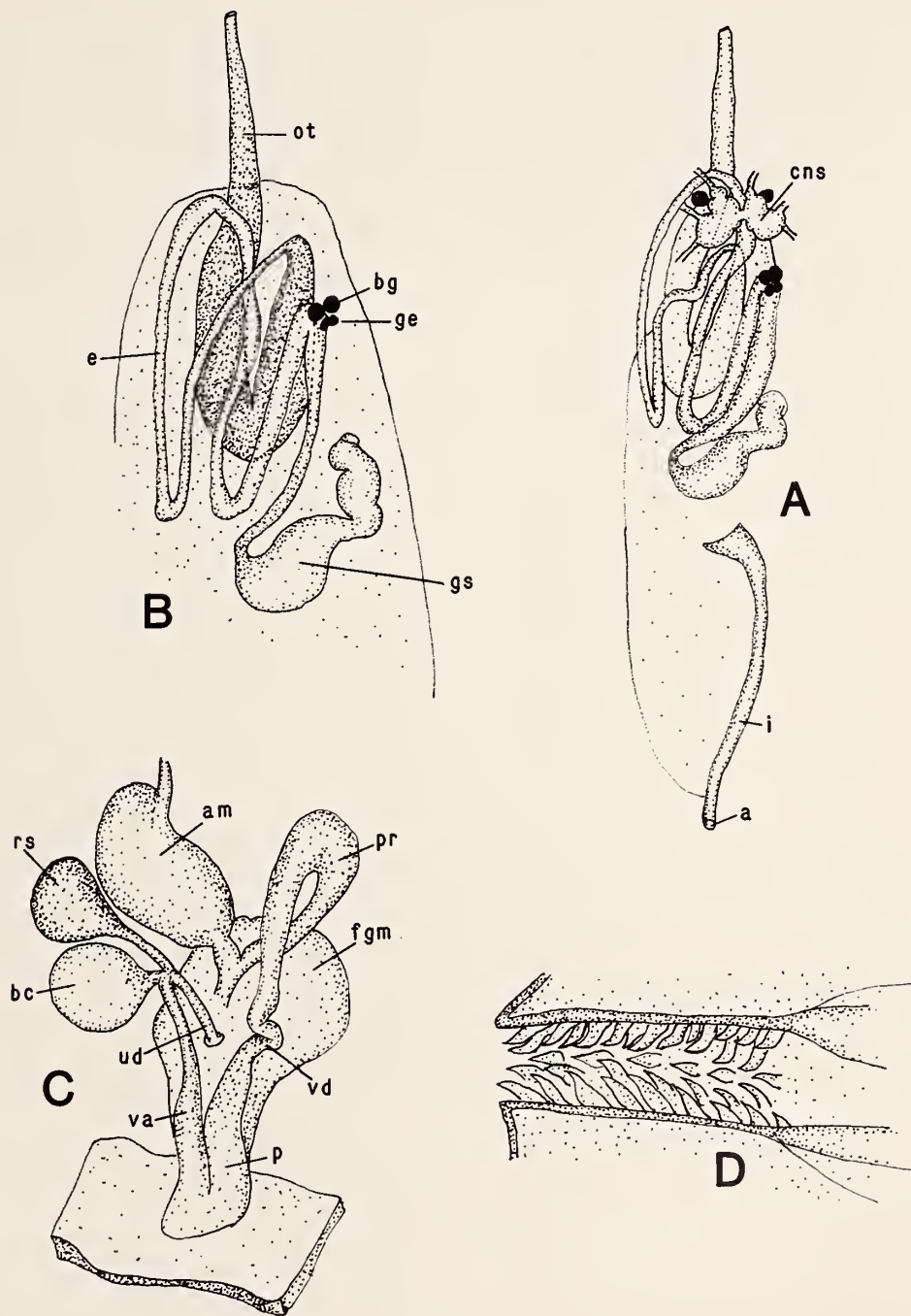


Figure 5

*Phyllidiopsis blanca* sp. nov. A. Digestive system with central nervous system: a, anus; cns, central nervous system; i, intestine. B. Detail of digestive system with central nervous system removed: bg, buccal ganglia; e, esophagus; ge, gastro-esophageal ganglia; gs, glandular segment of esophagus; ot, oral tube. C. Reproductive system: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; p, penis; pr, prostate; rs, receptaculum seminis; ud, uterine duct; va, vagina; vd, vas deferens. D. Penial armature.



**Digestive system (Figures 5A, B):** The oral tube is narrowest at the mouth, gradually widening posteriorly. The oral tube is simple throughout its length and is devoid of associated oral glands. It recurves anteriorly and narrows abruptly into the esophagus. The esophagus consists of several convolutions, which traverse the length of the oral tube. Near its posterior limit, the esophagus expands into a glandular segment, curves anteriorly, and enters the digestive gland. More posteriorly, the intestine emerges again from the digestive gland and continues posteriorly to its termination at the anus.

**Central nervous system:** The ganglia constituting the circumesophageal nerve ring are highly concentrated. The paired cerebral and pleural ganglia are largely fused. The cerebral ganglia are appressed to each other, without a distinctly narrowed commissure. The pedal ganglia are separated by a short commissure. Extending posteriorly from the cerebro-pleural ganglia are the elongate buccal nerves. They are joined to the paired buccal ganglia along the sides of the esophagus. Immediately posterior to the buccal ganglia are the gastro-esophageal ganglia. In one specimen the buccal and gastro-esophageal ganglia are situated near the posteriormost loop of the esophagus. In a second specimen, they are situated even more posteriorly, just anterior to the glandular swelling of the esophagus.

**Reproductive system (Figure 5C):** The reproductive system is triaulic. The ampulla is short and saccate. Proximally, it narrows into the postampullary duct just prior to its bifurcation into the oviduct and vas deferens. The oviduct enters the female gland mass after a short distance. The various nidamental glands that constitute the female gland mass cannot be differentiated, owing to poor preservation. The uterine duct emerges from the female gland mass near its juncture with the oviduct. It joins the receptaculum seminis and bursa copulatrix at their common base. The receptaculum has a short duct while the bursa is inserted directly on to the uterine duct. Emerging from the proximal end of the juncture of the uterine duct, receptaculum, and bursa, is the vaginal duct. It is elongate and widens gradually towards the gonopore. The vas deferens is prostatic distally following its separation from the oviduct at the proximal terminus of the postampullary duct. It narrows into a muscular ejaculatory segment that terminates adjacent to the vaginal and nidamental openings. The proximal end of the ejaculatory segment (Figure 5D) contains 4 or 5 rows of sharp, chitinous spines, with approximately 12 spines per row.

**Discussion:** *Phyllidiopsis blanca* is placed in *Phyllidiopsis* because it lacks a ring of oral glands present in *Phyllidia* and *Reyfra*. The presence of a ventral anus in one specimen of *P. blanca* represents an acquisition of this character independently from that of *Reyfra*.

The known morphology of species of *Phyllidiopsis* is compared in Table 1. *Phyllidiopsis blanca* and *P. berghi* Vayssi re, 1902, are the only known species within the

family that have uniformly whitish coloration. All other species have complex color patterns and, with the exceptions of *P. cardinalis* and *P. tuberculata*, possess some black pigment on the notum. *Phyllidiopsis berghi* differs from *P. blanca* in having a distinct vestibule at the anterior end of the oral tube and a much longer oral tube (BOUCHET, 1977:fig. 17). *Phyllidiopsis blanca* is also similar to *P. gynenopla* Bouchet, 1977, in its arrangement of the digestive system, but lacks the distinct armature surrounding the nidamental opening of the female reproductive system.

#### DISCUSSION OF GENERA

The distinctions between genera within the Phyllidiidae have been discussed by several workers (BERGH, 1875, 1889; PRUVOT-FOL, 1956, 1957; MARCUS & MARCUS, 1962; EDMUNDS, 1972; W GELE, 1985; YONOW, 1986). The major characteristics utilized to separate genera are the elaboration of the oral tube and associated glands, the position of the anus, and the elaboration of the oral tentacles.

Most studies have differentiated *Phyllidia* and *Reyfra* (as *Fryeria*) from *Phyllidiopsis* and *Ceratophyllidia* on the basis of the possession of a large mass of oral glands surrounding the oral tube in the former two genera.

In *Phyllidiopsis* and *Ceratophyllidia* the arrangement of oral glands, when present, is more complex. The type species of *Phyllidiopsis*, *P. cardinalis* Bergh, 1875, and most other members of the genus lack oral glands (Table 1), as in *P. blanca*. *Phyllidiopsis papilligera* Bergh, 1890 (MARCUS & MARCUS, 1962:fig. 24) and *P. molaensis* have a single nodular oral gland, which enters the posterior end of the oral tube. In *P. papilligera* there is a caecum at the distal end of the gland that is absent in *P. molaensis*. *Phyllidiopsis tuberculata* (RISBEC, 1928) was reported to have a large oral gland, but PRUVOT-FOL (1957) has suggested that this is actually the blood gland. There is some question as to whether *P. tuberculata* may actually be a junior synonym of *P. cardinalis* Bergh, 1875. Both species have compound tubercles and are similar in their coloration. *Ceratophyllidia africana* has a pair of large oral glands with ducts entering the oral tube and running its length adjacent to the esophagus (ELIOT, 1903; present study).

*Phyllidia* has also been characterized by having well developed retractor muscles, while they are apparently absent in *Phyllidiopsis* (PRUVOT-FOL, 1957). On the basis of lacking retractor muscles, EDMUNDS (1972) placed a phyllidiid species in *Phyllidiopsis*, despite the fact that it had prominent oral glands surrounding the oral tube. Similarly, *Ceratophyllidia africana* has large retractor muscles but lacks a ring of distinct glands. Thus, the presence of both a mass of oral glands and retractor muscles cannot be used to separate *Phyllidia* from *Phyllidiopsis* and *Ceratophyllidia*. It seems that the mass of oral glands in *Phyllidia* and *Reyfra* is far more likely to represent a unique derivation within the Phyllidiidae, and should be afforded greater weight in differentiating these genera from *Phyl-*



Table 1  
Morphological variability of *Phyllidiopsis*.

	Distribution	Tubercles	Oral tentacles	Oral tube	Oral glands	Cerebro-buccal connective	Gills	Vas deferens	References
<i>P. cardinalis</i>	Indo-Pacific	compound	largely fused	no vestibule	absent	elongate	75 +	unarmed	PRUVOT-FOL, 1957; present study
<i>P. tuberculata</i>	New Caledonia	compound	—	with large vestibule	absent ?	—	—	—	RISBEC, 1928; PRUVOT-FOL, 1957
<i>P. papilligera</i>	W. Atlantic	simple, low warts	round, largely fused	thick vestibule	present ventral	elongate	100 per side	armed	BERGH, 1890; MARGUS & MEYER, 1977
<i>P. molaensis</i>	Atlantic coast	simple, conical	conical, separate	thick vestibule	present dorsal	—	—	—	MARGUS & MEYER, 1977
<i>P. bergii</i>	of Panama	simple, round	short, united at base	with thickener vestibule	absent	elongate	70-80 per side	armed	VAYSSIÈRE, 1902; BOUCHET, 1977
<i>P. gemmata</i>	?	simple, round	largely united	no vestibule	absent	elongate with buccal glands situated anterior to nerve ring	numerous	—	PRUVOT-FOL, 1957
<i>P. krempfi</i>	Viet Nam	compound	united	with thickener vestibule	absent	—	—	—	PRUVOT-FOL, 1957
<i>P. striata</i>	Thailand	simple, conical	short, separate	no vestibule	present ?	elongate	—	armed	BERGH, 1889
<i>P. gynecopla</i>	E. Atlantic	simple, hemispherical	largely united	no vestibule	absent	elongate	—	armed	BOUCHET, 1977
<i>P. blanca</i>	E. Atlantic	simple, round	united throughout	no vestibule	absent	elongate	60-70 per side	armed	present study

*lidiopsis* and *Ceratophyllidia*. Hence, EDMUNDS' (1972) species should be placed in *Phyllidia*.

The systematic position of *Ceratophyllidia* has been the subject of confusion. Since its original description (ELIOT, 1903), most workers have considered *Ceratophyllidia* as a junior synonym of *Phyllidiopsis* (THIELE, 1931; PRUVOT-FOL, 1957; FRANC, 1968). MARCUS & MARCUS (1962) suggested that *Ceratophyllidia* should be regarded as a distinct genus on the basis of its possession of stalked papillae. Unfortunately, the opinions regarding its generic status were based solely on ELIOT's incomplete descriptions (1903, 1910). Examination of the present material provides a more complete basis of comparison. The fleshy, stalked, readily detachable papillae are unique to *Ceratophyllidia*. Also the presence of paired oral glands with ducts running parallel to the esophagus within the oral tube is known only from *Ceratophyllidia*. This additional fact lends support to the contention that *Ceratophyllidia* represents a distinct genus.

The systematic position of *Fryeria* Gray, 1853, had never been in question. Recently, however, YONOW (1986) correctly pointed out that the name *Fryeria* had been incorrectly applied to *F. ruppelli* rather than to *Phyllidia pustulosa* Cuvier, 1804. She considered *Fryeria* as a junior synonym of *Phyllidia*, because *P. pustulosa* has a dorsal anus, and substituted the *Reyfriedia* for the species with a ventral anus. The fact that specimens of *Phyllidiopsis blanca* examined in this study are variable in the position of the anus (dorsal in five specimens, ventral in one) casts serious doubts as to whether *Reyfriedia* should be separated from *Phyllidia*. Certainly, the degree of intraspecific variability of this character within the Phyllidiidae must be examined in greater detail.

ELIOT (1903) stated that, although it was not possible to examine the vas deferens of *Ceratophyllidia africana*, it was likely that it was armed with hooks, as in other members of the family. THIELE (1931) also characterized the family as having spines within the male duct. However, WÄGELE (1985) observed that the male duct of *Phyllidia pulitzeri* lacked armature. Similarly, the type species of *Phyllidiopsis* and *Ceratophyllidia* also lack any armature (present study). It appears that this character varies within genera.

#### ACKNOWLEDGMENTS

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